

THE DISTRIBUTION OF BENTHIC INFAUNA OF A TEXAS SALT MARSH IN RELATION TO THE MARSH EDGE

Shannon D. Whaley¹ and Thomas J. Minello
*National Marine Fisheries Service
Southeast Fisheries Science Center
Galveston, Texas, USA 77551*

¹ *Present address:
Florida Marine Research Institute
100 Eighth Avenue Southeast
St Petersburg, Florida, USA 33701
E-mail: Shannon.Whaley@fwc.state.fl.us*

Abstract: Coastal salt marshes in the northern Gulf of Mexico are often highly fragmented, with a large amount of marsh edge, the interface between the vegetated marsh surface and shallow open water. Nekton predators, including many juvenile fishery species, aggregate near this marsh edge, and benthic infaunal populations are a primary source of prey for many of these predators. We examined the fine-scale (1–10 m) distributions of benthic infauna in relation to the edge of a Texas, USA salt marsh. Every six weeks for nearly a year, we sampled marsh sediments at five locations: on nonvegetated bottom 1 m from the marsh edge and on the vegetated marsh surface at 1, 3, 5, and 10 m from the edge. Surface-dwelling annelid worms and peracarid crustaceans were most abundant in low-elevation sediments near the marsh edge for most sampling periods. Because the marsh slope varied within the study area, we could distinguish between correlative relationships with elevation and distance from the marsh edge. Distributions of common surface-dwelling species were often unrelated to elevation but almost always negatively related to distance from the marsh edge. Abundances of near-surface direct deposit feeders and omnivores were related to both distance from edge and elevation. In contrast to surface dwellers, densities of abundant subsurface deposit feeders (mainly oligochaetes) were frequently greatest in sediments located away from the marsh edge. Surface and near-surface dwelling infauna are an important prey resource for nekton, including many juvenile fishery species that concentrate near the marsh edge. Populations of these infaunal prey fluctuated seasonally, with the greatest densities occurring during winter and early spring when predator abundances are generally low. Infaunal densities decreased dramatically near the marsh edge from the late spring through early fall, and this decrease coincides with historically high seasonal densities of nekton predators. Our data suggest that there is a strong trophic link between infauna and nekton near the marsh edge and that this relationship contributes to the high fishery productivity derived from Gulf Coast marshes.

Key Words: salt marsh, benthic infauna, polychaetes, edge, elevation, *Spartina alterniflora* marsh, oligochaetes

INTRODUCTION

Gulf Coast salt marshes are inhabited by many nekton species, and the marsh edge or interface between the vegetated marsh surface and shallow open water appears to be a center of activity for transient nekton, including important fishery species (Baltz et al. 1993, Minello et al. 1994, Peterson and Turner 1994, Minello 1999, Rozas and Zimmerman 2000, Minello and Rozas 2002). These juvenile nekton species often feed on benthic infauna (Kneib and Stiven 1978, Weisberg and Lotrich 1982, Minello and Zimmerman 1983, Minello et al. 1989, Thomas 1989, Rozas and LaSalle 1990, McTigue and Zimmerman 1998). Therefore, the

infaunal community represents a significant trophic link between nekton populations and primary production derived from the marsh (Currin et al. 1995, Kneib 1997a, 2000, Deegan et al. 2000, Kreeger and Newell 2000, Zimmerman et al. 2000). The abundance and productivity of infaunal organisms and their accessibility to nekton predators determines the extent and efficiency of this trophic link (Zimmerman et al. 2000).

The intertidal marsh alternately changes from an aquatic to a terrestrial environment, and this transformation is controlled by tidal dynamics and marsh topography. At increasing distances from the marsh edge and away from open water, the elevation of the marsh

surface generally increases, and the marsh environment is less frequently inundated. Small differences in elevation can dramatically vary the hydroperiod and modify living conditions for infauna within the intertidal zone, and elevation has been identified as an important factor affecting infaunal abundance in marshes (Kneib 1984, 1992, Moy and Levin 1991, Levin et al. 1996). There also is some evidence that distance from the marsh edge is important for infauna; when elevation was controlled in a field experiment, the abundance of infaunal organisms was related to distance from the marsh edge (Minello et al. 1994).

Despite their apparent importance as prey for fishery species, relatively little is known about the distributions of benthic infauna in salt marshes of the northern Gulf of Mexico. Our objective was to examine the fine-scale (1–10 m) distributions of infauna in relation to the edge of a Texas salt marsh. We sampled sediments every six weeks for nearly a year at five different distances from the edge. The slope of the marsh surface along this edge varied; thus, the data also provided some insight into the relative importance of distance from the edge versus elevation in determining infaunal abundance. We also examined flooding duration and sediment organic content, temperature, and grain size as potential factors influencing infaunal abundance.

METHODS

The Study Area

The study area is a polyhaline *Spartina alterniflora* Loisel (smooth cordgrass) marsh located near Gang's Bayou on the western end of Galveston Island, a barrier island on the upper Texas coast separating the Galveston Bay System from the Gulf of Mexico (Figure 1). Marshes on the bay side of such islands are generally created and nourished by the deposition of storm-driven overwash sediments from the Gulf of Mexico. Between these long-term storm events (decades to centuries), the marshes undergo degradation due to subsidence and erosion. These degrading marshes are highly fragmented, with a large amount of marsh edge (Minello and Rozas 2002). Substantial marsh berms (creekside or marsh edge levees) are uncommon in these barrier island marshes. Our study area consisted of 1 km of shoreline with a variable slope from the marsh edge to the inner marsh. A small (5–10 cm in elevation) berm existed in some areas, but for the most part, elevation increased with distance from the edge.

We sampled benthic infauna in sediments at five different locations in relation to the marsh edge (Figure 1). The marsh edge was identified as the interface

between the marsh vegetation and the open water of the pond. *Spartina alterniflora* shoot density was high on the edge, making this boundary distinctive. Sediments were sampled at one location outside of the vegetation at 1 m from the marsh edge (–1m location). Other locations were within marsh vegetation at successively greater distances from the marsh edge (+1m, +3m, +5m, +10m). In a companion study, Minello and Rozas (2002) sampled nekton within vegetation at the same four marsh locations in the spring (May 30–June 1) and fall (Oct 3–4) using an enclosure device.

Collection of Marsh Infauna and Sediment Samples

We collected 125 infaunal sediment cores (5-cm diameter to a depth of 5 cm) every six weeks from February 22 through November 11, 1995; 25 sites were selected randomly along the 1-km shoreline for each of the five sampling locations (Figure 1). The appropriate sampling effort was determined by applying a power analysis to similar infauna data taken in a nearby marsh; 25 samples per location were projected to allow detection of at least a 50% difference in location means (Sokal and Rohlf 1981). Sediment cores were taken without regard to the presence of vegetation; when present, plant stems were counted and snipped off at the mud line before the core was collected. Thus, our data represent only benthic infaunal abundances and do not include epiphytic organisms associated with plant stems. The core tube was inserted into the sediment to a depth of at least 10 cm and carefully sealed at the bottom with the palm of a hand before removal. The upper 5 cm of sediment was retained for analysis. During the first sampling period in February, two additional sediment core samples (3-cm diameter, 5-cm depth) were taken per sample site to compare sediment grain size and organic content (SOC) among locations. All core samples were placed in plastic bags, stored on ice, and returned to the laboratory for further processing.

We determined elevation at each sampling site by measuring the water level at the time each sample was collected and comparing these values to concurrent water-level measurements on a permanent staff gauge in Gang's Bayou (Figure 1). With the exception of the February collection, sampling occurred at high tide when the entire intertidal zone was inundated and water levels for all sites could be recorded. In February, tides were rarely high enough to cover the entire marsh. Therefore, samples were taken with the marsh exposed, and sample sites were marked with stakes. Elevations of these sites were measured three weeks later when the entire marsh surface was flooded. To monitor inundation patterns in the sampling area, water levels were recorded every hour during the study

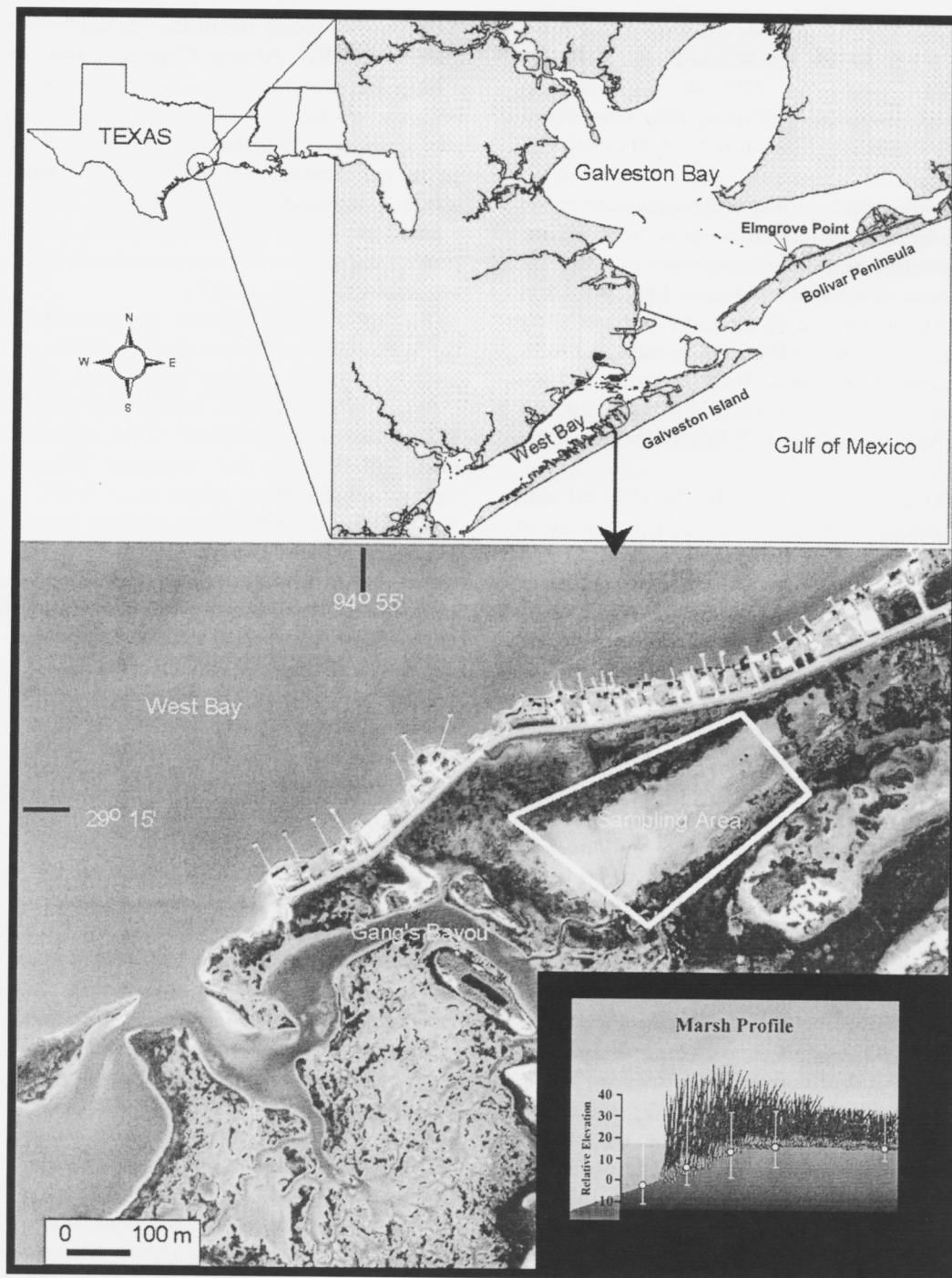


Figure 1. Map of the Gang's Bayou sampling area located off West Bay in the Galveston Bay system of Texas. The area within the white polygon contains the 1 km of shoreline that was sampled. Asterisk indicates location of water-level recorder. Within the marsh profile, circles denote mean relative elevations along the five locations that were sampled; error bars indicate the elevation range for each location.

(Remote Data Systems WL40TM water-level recorder) (Figure 1). The water-level recorder was positioned in close proximity to the sampling area (200 meters away) and next to our permanent staff gauge. Water levels were recorded on the staff gauge before and after each sampling event, and these measurements

were used to calibrate recorded water levels. On October 4, 1995, extremely high water levels caused by Hurricane Opal damaged our recorder. Water-level data following this event were extrapolated from levels measured at NOAA tide station No. 887-1450 in the Galveston Ship Channel (29° 18.6' N and 94° 47.6'

W) approximately 12.5 kilometers from the study area. The relationship between water levels (cm) at Gang's Bayou (GBWL) and the NOAA tide station (NOAAWL) was determined by using data from April to August, 1995 ($GBWL(cm) = 0.539 * NOAAWL - 17.080$, $r=0.63$).

Water temperature and salinity were measured hourly using a Hydrolab Datasonde located next to our water-level recorder. Sediment temperatures were recorded every hour (Onset HOBO data loggers) 1 cm below the sediment surface in three of the sampling locations: -1m, +1m, and +10m. Daily mean air temperatures were obtained from a NOAA weather station (No. 12923) located at Scholes Field Air Base (29° 18' N and 94° 48' W) in Galveston, 8 kilometers from the sampling area.

In the laboratory, core samples for benthic infauna were sieved through a 500- μ m mesh and preserved in 10% formalin with rose bengal stain. Annelids, small crustaceans, and mollusks were identified to species or to the lowest feasible taxonomic level, counted, dried (at 100°C for 24 hours), and weighed. Sediment macroorganic matter (MOM) in each location was determined from infaunal core samples collected during July. Small amounts of shell present in the samples were removed before analysis. After organisms were removed from sieved samples, material that appeared to be living at the time of collection (LMOM) was separated from detritus (DMOM) under a dissecting microscope. This material was oven-dried for 24 hours at 100°C and weighed to determine dry biomass. Sediment organic content (SOC) was determined by the ignition loss method (Dean 1974). The SOC cores were wet-sieved through a 2-mm mesh to remove stems and roots, air-dried under a vacuum hood to remove most of the water, ground with mortar and pestle, placed in pre-weighed ceramic crucibles, and dried at 110°C for 24 hours to remove remaining interstitial water. Samples were transported in a desiccation chamber to be weighed, burned in a muffle furnace at 375°C for four hours, cooled in a desiccation chamber, and re-weighed. Sediment grain size was analyzed using the sieving and pipette techniques described by Folk (1980). We sampled sediment grain size and organic content (February) and below-ground macroorganic material (July) only once during the year because these sediment characteristics remain relatively constant on an annual time scale in well established natural marshes (Whitlatch 1981).

Statistical Analyses

A $\ln(y+1)$ transformation of the infaunal abundance data was used to correct heteroscedasticity (F-max tests), and a one-way ANOVA was used to test for

differences among locations for each sampling period (SuperANOVA, Abacus Concepts, Inc., Berkeley, CA, 1989). Separate analyses were conducted for overall infauna, overall polychaetes, *Capitella* spp., *Streblospio benedicti*, *Laonereis culveri*, oligochaetes, and peracarid crustaceans; the sequential Bonferroni technique, as described by Rice (1988), was used to adjust significant levels for multiple tests. We used *a priori* linear contrasts to make comparisons of interest among locations.

For the overall infaunal community, we examined the importance of elevation in addition to the effect of location within marsh vegetation (locations +1m, +3m, +5m, +10m) by conducting a multivariate analysis of covariance (MANCOVA with Wilk's lambda) using elevation as the covariate. When there was no significant elevation effect ($p > 0.05$) in preliminary tests, we used multivariate analysis of variance (MANOVA) to test for edge effects on the benthic community. These multivariate statistics were used to take into account the interdependence of individual species abundances and larger taxonomic groups used as dependent variables in our analyses.

RESULTS

Distribution of Benthic Infauna among Locations

Polychaetes (51.7 %), oligochaetes (32.5 %), and peracarid crustaceans (14.5 %) were the most abundant organisms in sediment cores (Table 1). Abundances varied through the year and among locations. Greatest densities generally occurred in the winter and spring, with low densities during August through October (Figures 2 and 3). The most abundant organisms in samples were the surface-dwelling infauna, including suspension feeders and surface deposit feeders (infauna feeding on deposits on the sediment surface). These infauna were most prevalent at the +1m location, making up 55% of all annelids, crustaceans, and mollusks (Table 1). Subsurface deposit feeders (infauna feeding on deposits below the sediment surface) were most prevalent at the +3m (65% of organisms), +5m (74%), and +10m (83%) locations. The nonvegetated location (-1m) had similar proportions of surface (43%) and subsurface (43%) deposit feeders. Omnivorous species accounted for 14% of organisms at -1m but only 5 to 7% at vegetated locations. Species richness was similar among the locations (Table 1).

During spring and early summer, overall densities of benthic infauna within vegetation were generally greatest near the marsh edge (Figure 2). However, these densities decreased in summer and early fall, and differences among locations were reduced; by October, there were few significant differences in overall infauna

Table 1. Density of benthic infauna (per 19.6-cm² core) in cores collected at five locations: -1 m (nonvegetated), and +1 m, +3 m, +5 m, +10 m within the marsh in Gang's Bayou. Biomass values for major taxa are also presented at the end of the table. Annual means are calculated from 175 cores collected at each of the five locations over all seven sampling periods throughout the year of 1995. The number of species listed represents the total number of species collected (within the polychaetes, crustaceans, and mollusks) for each location. Feeding mode was determined for annelids, crustaceans, and mollusks according to Bousfield (1973), Andrews (1981), Heard (1982), and Gaston et al. (1988): D = direct deposit feeders (subsurface), Su = suspension feeder, SD = surface deposit feeder, O = omnivore, C = carnivore.

Distance from the Marsh Edge:	Feeding Mode	-1	+1	+3	+5	+10	Total Abundance
Total infauna		31.99	63.23	32.44	26.91	26.20	31629
Annelida		27.56	46.45	28.57	24.94	24.76	26649
Polychaeta		23.10	34.04	15.51	11.37	9.43	16356
<i>Capitella</i> spp.	D	8.59	11.90	7.75	6.14	5.69	7012
<i>Streblospio benedicti</i> Webster, 1879	SuSD	8.89	17.33	5.19	3.05	1.86	6358
<i>Laeonereis culveri</i> (Webster, 1879)	O	4.49	3.41	1.53	1.70	1.50	2208
<i>Sabella</i> spp.	Su	0.13	0.75	0.84	0.31	0.26	401
<i>Leitoscoloplos foliosus</i> Day, 1977	D	0.54	0.03	0.00	0.00	0.00	101
<i>Neanthes succinea</i> Frey and Leuckart, 1847	C	0.07	0.23	0.09	0.11	0.08	100
<i>Polydora cornuta</i> (Bosc, 1802)	SD	0.14	0.25	0.05	0.02	0.01	80
<i>Melinna maculata</i> Webster, 1879	SD	0.12	0.10	0.05	0.03	0.04	59
<i>Heteromastus filiformis</i> (Claparede, 1864)	D	0.08	0.01	0.01	0.00	0.00	17
<i>Marphysa sanguinea</i> (Montagu, 1815)	C	0.00	0.02	0.01	0.01	0.00	6
<i>Scoloplos fragilis</i> (Verrill, 1878)	D	0.03	0.00	0.00	0.00	0.00	5
<i>Mediomastus</i> spp.	D	0.02	0.00	0.01	0.00	0.00	4
<i>Arenicola cristata</i> Stimpson	D	0.01	0.00	0.00	0.00	0.00	2
<i>Eteone heteropoda</i> Hartman	C	0.00	0.01	0.00	0.00	0.00	2
<i>Scolecipis texana</i> Foster, 1971		0.00	0.00	0.00	0.01	0.00	1
Oligochaeta	D	4.46	12.41	13.06	13.57	15.33	10293
Crustacea		4.31	16.15	3.33	1.54	0.83	4573
<i>Hargeria rapax</i> (Harger, 1879)	SD	0.72	10.33	2.19	0.86	0.38	2535
<i>Corophium</i> spp.	SD	2.59	4.93	0.62	0.24	0.13	1489
<i>Gammarus mucronatus</i> Say, 1818	SD	0.18	0.50	0.41	0.39	0.29	310
<i>Ampelisca</i> spp.	SuSD	0.40	0.16	0.02	0.02	0.01	108
<i>Grandidierella bonnieroides</i> Stephensen, 1947	SD	0.29	0.14	0.04	0.02	0.02	88
<i>Edotea montosa</i> (Stimpson, 1853)		0.02	0.00	0.00	0.00	0.00	3
Mollusca		0.05	0.14	0.10	0.10	0.08	82
<i>Cerithidea pliculosa</i> (Manke, 1829)	SD	0.05	0.05	0.03	0.07	0.08	49
F. Hydrobiidae	SD	0.00	0.05	0.06	0.02	0.00	22
<i>Geukensia demissa</i> (Dillwyn, 1817)	Su	0.00	0.04	0.01	0.01	0.00	10
<i>Chione cancellata</i> (Linnaeus, 1767)	Su	0.00	0.01	0.00	0.00	0.00	1
Nudibranchia		0.00	0.01	0.01	0.00	0.00	3
Number of species		19	19	17	16	13	29
Other		0.07	0.48	0.45	0.33	0.53	325
Infaunal biomass		6.59	7.80	3.22	2.30	1.91	3893.20
Annelid biomass (mg)		5.88	6.79	2.78	1.93	1.72	3412.70
Crustacean biomass (mg)		0.51	0.82	0.30	0.17	0.08	330.50
Other biomass (mg)		0.21	0.19	0.14	0.21	0.11	150.00

nal density among the five locations (Figure 2, Table 2). In early spring, densities at -1m (nonvegetated bottom) were relatively high and not significantly different from those at the +1m location. However, densities at -1m decreased earlier than at +1m, and there was a significant difference between the two locations by the April 3 sampling period. Numbers of infauna at all locations increased in the late fall (November 22

sampling period), and mean densities were again greatest near the marsh edge (Figure 2).

The seasonal pattern for the most common polychaetes (*Capitella* spp., *Streblospio benedicti*) and peracarid crustaceans (primarily *Hargeria rapax*) reflected the seasonal pattern for overall infauna (Figures 2 and 3). However, the ratio of individuals at the +1m location near the marsh edge compared with other lo-

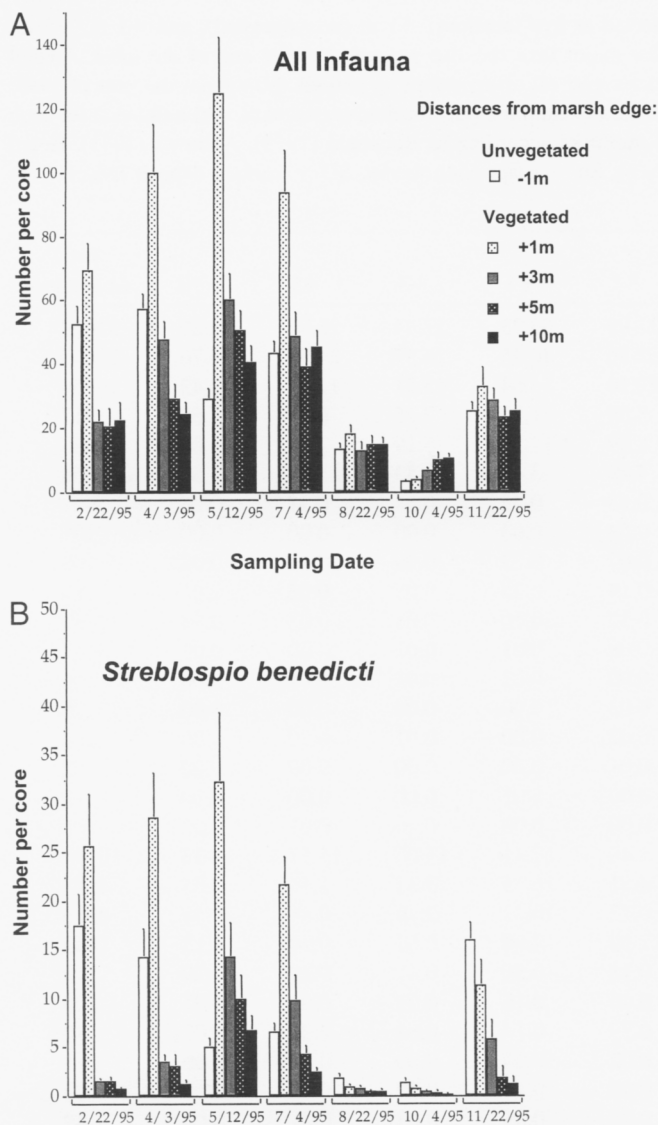


Figure 2. Mean densities of all infauna and *Streptosio benedicti* at the five locations for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core has a surface area of 19.6 cm² and a depth of 5 cm.

cations varied greatly in magnitude among these taxonomic groups. *Streptosio benedicti* and peracarid crustaceans were mainly found at +1m; mean densities here often reached levels more than twice as great as in any other location. In May, mean densities of peracarid crustaceans at +1m were more than five times greater than those at any other location. Although abundances of *Capitella* spp. were also greatest at +1m for most of the year, differences among locations were not as large as differences for *S. benedicti* and peracarid crustaceans. In contrast to most other infauna, oligochaetes were distributed more evenly among marsh locations. Densities were consistently greater in

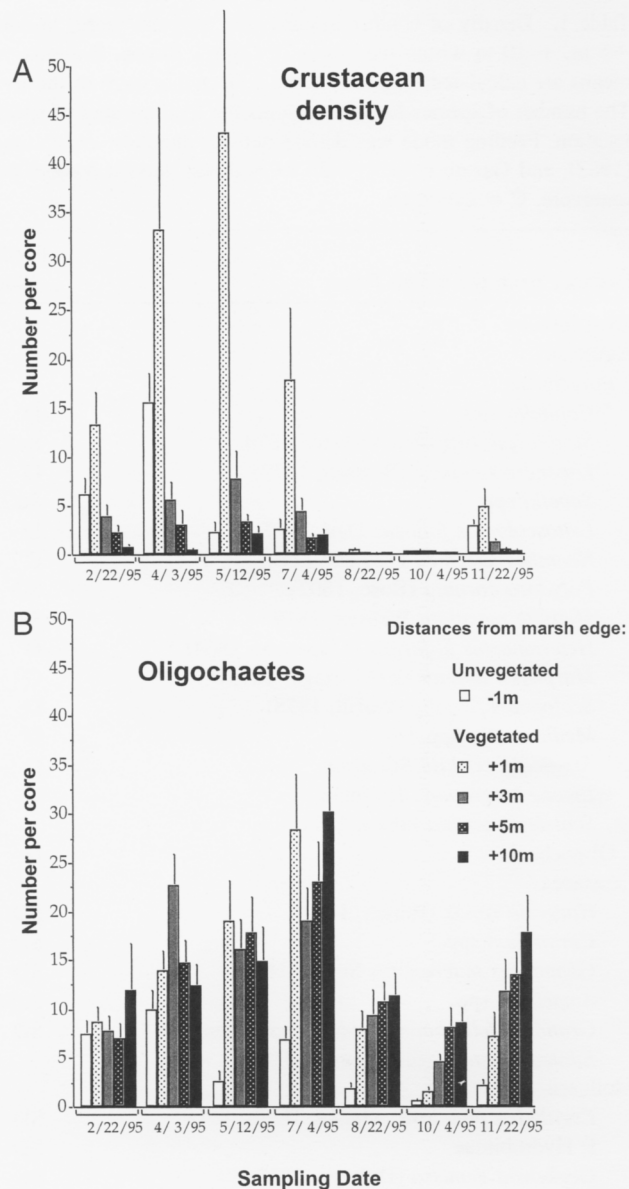


Figure 3. Mean densities of peracarid crustaceans and oligochaetes among the five locations for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.

sediments from the vegetated marsh surface than in nonvegetated sediments, and mean oligochaete densities were frequently greatest farthest (+10m) from the marsh edge (Figure 3).

Patterns of annelid and crustacean biomass were generally similar to abundance patterns, and the +1m location had the greatest biomass within vegetated sediments (Table 2, Figure 4). In April and May, however, the highest annelid biomass occurred in nonvegetated sediments, while annelid density was greatest in vegetation. This difference occurred because *Lae-*

Table 2. Results from one-way ANOVAs comparing infaunal densities among five locations (Edge effect). Analyses on biomass of annelids and crustaceans are also included. Degrees of freedom are total (124), main effect of Edge (4), and residual error (120). Data for each month were analyzed independently. Alpha levels were adjusted using the Sequential Bonferroni technique (Rice 1988) to account for multiple tests. Three asterisks denote significance at an adjusted alpha level of less than 0.0001. P-values greater than 0.0001 are listed. Two asterisks denote significance at an adjusted alpha level of 0.001, and one asterisk denotes significance at an adjusted alpha level of 0.05.

	February		April		May		July		August		October		November	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value
Total infauna	15.25	***	13.88	***	9.66	***	5.64	***	0.39	0.8127	8.29	***	0.99	0.4127
Polychaetes	28.42	***	24.82	***	6.83	***	15.61	***	11.34	***	0.35	0.8417	15.09	***
<i>Capitella capitata</i>	11.37	***	11.91	***	3.25	0.0146*	7.43	***	8.15	***	1.40	0.2376	5.72	0.0003***
<i>Sireblosipio benedicti</i>	35.82	***	38.34	***	15.35	***	17.86	***	4.99	0.0009**	4.09	0.0037*	32.01	***
<i>Laeonereis culveri</i>	8.15	***	6.01	0.0002***	5.98	***	16.12	***	9.87	***	0.94	0.4427	1.59	0.1804
Oligochaetes	0.55	0.6946	5.23	0.0007***	19.07	***	11.75	***	11.20	***	15.07	***	15.17	***
Crustaceans	13.56	***	41.02	***	26.55	***	8.80	***	1.63	—	0.86	0.4891	7.64	***
Annelid biomass (mg)	13.86	***	13.61	***	4.02	0.0040*	6.11	0.0002**	11.36	***	0.18	0.9476	2.84	0.0272
Crustacean biomass (mg)	4.71	0.0013*	6.87	***	3.52	***	0.93	0.4564	0.34	0.8533	1.28	0.2809	4.65	0.0016*

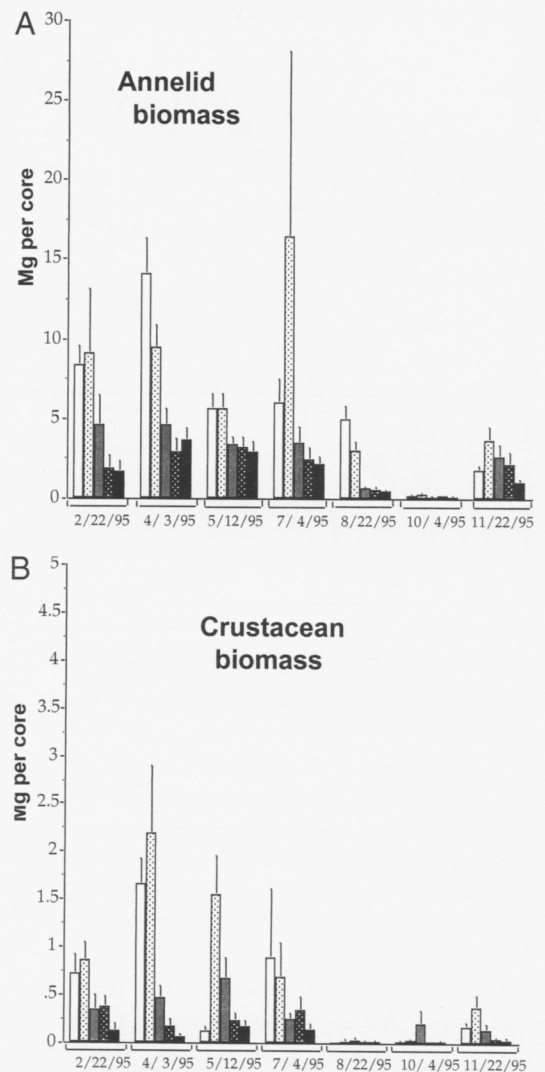


Figure 4. Mean biomasses of annelids and peracarid crustaceans among the five locations for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.

onereis culveri, a large omnivorous polychaete, was abundant in the nonvegetated cores (Table 1).

Edge and Elevation Effects on Infauna Distribution

Among the four vegetated locations, the importance of distance to the edge in relation to elevation varied over the sampling periods. In the multivariate analyses, there was a significant negative linear relationship between infaunal abundance and elevation during four of the seven sampling periods (February $F_{8,88} = 4.075$, $p = 0.0005$, April $F_{8,88} = 11.62$, $p = 0.0001$, July $F_{8,88} = 5.289$, $p = 0.0001$, and November $F_{8,88} = 3.1630$, $p = 0.0035$). Throughout the year, however, there was a constant and highly significant relationship between

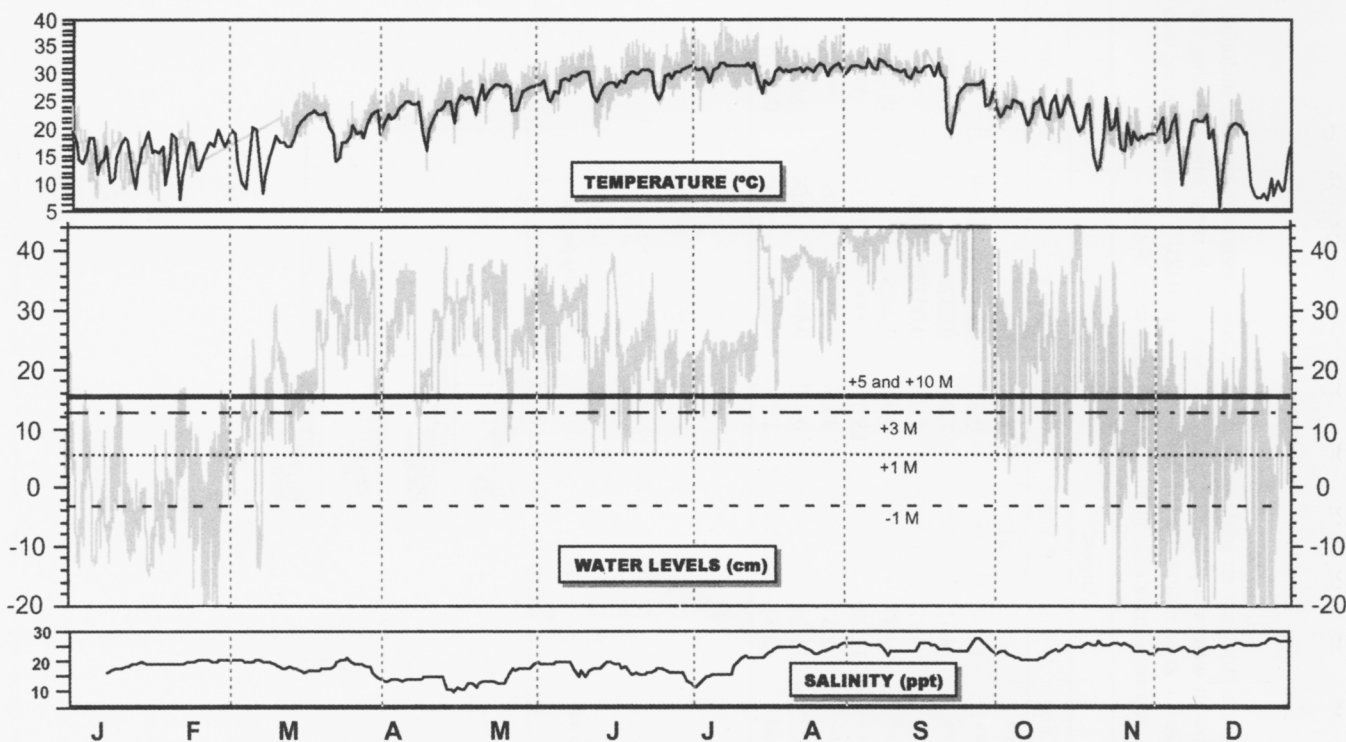


Figure 5. Temperature, water level, and salinity measured at Gang's Bayou from January 11 to December 31, 1995. Starting from October 4 through December 31, water levels at the sample site were extrapolated from levels measured at NOAA tide station #887-1450 in the Galveston Ship Channel (29° 18.6' N and 94° 47.6' W). Dotted vertical lines indicate sampling periods. Hourly water temperature (gray line) was plotted with daily mean air temperatures (black line). In the middle graph, dark gray lines represent hourly water levels. Horizontal lines are mean relative elevation for each of the five locations sampled. Daily mean salinities for 1995 were calculated from hourly data.

infaunal abundance and distance from the marsh edge after adjusting for significant elevation effects (February $F_{24,256} = 1.703$, $p = 0.0241$, April $F_{24,247} = 2.399$, $p = 0.0004$, May $F_{24,259} = 2.707$, $p = 0.0001$, July $F_{24,256} = 2.368$, $p = 0.0005$, August $F_{24,259} = 2.795$, $p = 0.0001$, October $F_{24,259} = 2.001$, $p = 0.0046$, November $F_{24,247} = 2.253$, $p = 0.0224$). Infaunal abundance was negatively related to distance from the marsh edge for all sampling periods except during October when the relationship between infaunal abundance and distance from the marsh edge became positive due to the prevalence of oligochaetes and seasonally low densities of surface dwelling infauna (Figures 2 and 3). Elevation was seldom significant (alpha level of 0.05) in explaining distributions of abundant surface dwellers such as the polychaete *S. benedicti* and peracarid crustaceans, but these species were negatively related to distance from the edge throughout most of the year (*S. benedicti*: February $F_{3,96} = 10.5532$, $p = 0.0001$, April $F_{3,96} = 11.7092$, $p = 0.0001$, May $F_{3,96} = 13.0235$, $p = 0.0001$, July $F_{3,96} = 9.2013$, $p = 0.0001$, August $F_{3,96} = 4.1099$, $p = 0.0086$, November $F_{3,96} = 8.6939$, $p = 0.0001$, peracarid crustaceans: February $F_{3,96} = 8.3601$, $p = 0.0001$, May $F_{3,96} = 20.3741$, $p = 0.0001$, July $F_{3,96}$

$= 7.2351$, $p = 0.0002$, August $F_{3,96} = 3.3354$, $p = 0.0226$, November $F_{3,96} = 2.7747$, $p = 0.0455$, Figures 2 and 3). When elevation was significant, an edge effect was still generally present after the elevation effect was removed. Edge effects were generally not significant for *L. culveri* or oligochaetes. The abundance of oligochaetes was positively related to elevation in the spring and fall (Figure 3).

Physical/Chemical Factors and Sediment Characteristics

Salinity ranged from a low of 9.8 ppt in April to a high of 28.2 ppt in September and December (Figure 5). Sharp drops in salinity in the late spring and summer corresponded to the occurrence of local rainstorms. Salinity gradually increased through the fall and winter. Water temperature ranged from a low of 5 °C in December to a high of 39 °C in July. Sediment temperature varied among locations, and daily fluctuations generally increased with increasing elevation and decreasing water depth (Figure 6). Therefore, the most stable temperatures usually occurred in the non-vegetated sediment (-1m), and the widest sediment temperature fluctuations occurred ten meters from the

Sediment Temperatures (°C)

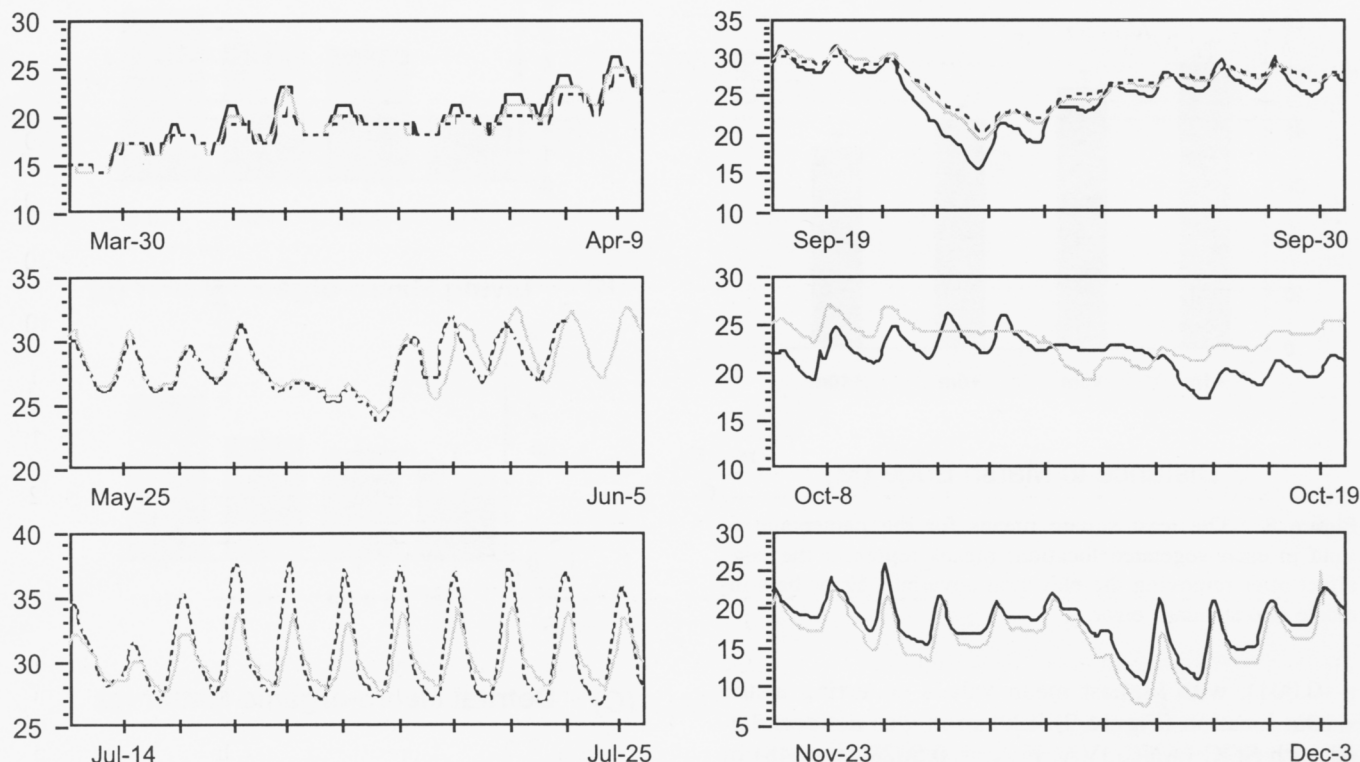


Figure 6. Typical daily sediment temperature fluctuations for three locations within the intertidal salt marsh at Gang's Bayou: nonvegetated location (-1m) = dotted line, $+1\text{m}$ location = gray line, and $+10\text{m}$ location = black line. Tick marks indicate 12:00 noon. The ranges of temperature fluctuation (y-axes) are different for each graph. Data from all three locations are not available for all time periods due to sensor malfunctions.

marsh edge ($+10\text{m}$). From May through July, however, temperatures in nonvegetated sediment were often similar or higher than temperatures at the $+1\text{m}$ location. The vegetation may have shaded sediments and moderated temperatures within the marsh during the summer.

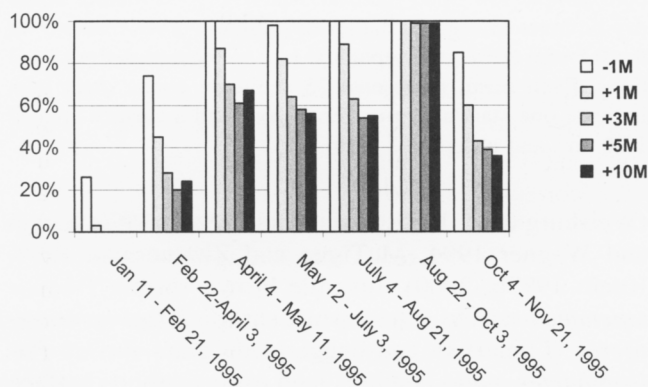


Figure 7. Extent of tidal inundation at each location. The mean percentage of time that a location was flooded in 1995 is shown for each six-week period between sampling events.

Water levels were lowest in the winter, and they peaked in spring and early fall (Figure 5). From near the end of July through the beginning of October, water levels were consistently high due to the presence of Tropical Storm Dean and Hurricane Opal in the Gulf of Mexico. Seasonal variability of inundation patterns was large (Figure 7). In January/February, for example, vegetated locations were inundated less than 3% of the time, and the nonvegetated location was only inundated 26% of the time. In contrast, during August/October, all locations were inundated for over 99% of the time.

The proportion of sand-sized particles varied among vegetated locations and was related to both elevation (ANCOVA, $F_{1,96} = 5.597$, $p=0.002$) and distance to the marsh edge (ANCOVA, $F_{3,96} = 4.078$, $p=0.009$). After removing elevation effects, the highest least square mean percentage of sand-sized particles was found at the $+1\text{m}$ location (Figure 8). There was a significant edge effect for sediment organic content (SOC) and the amount of below-ground living macroorganic matter (LMOM, ANCOVA, $F_{3,96} = 5.8956$,

Percent Sand

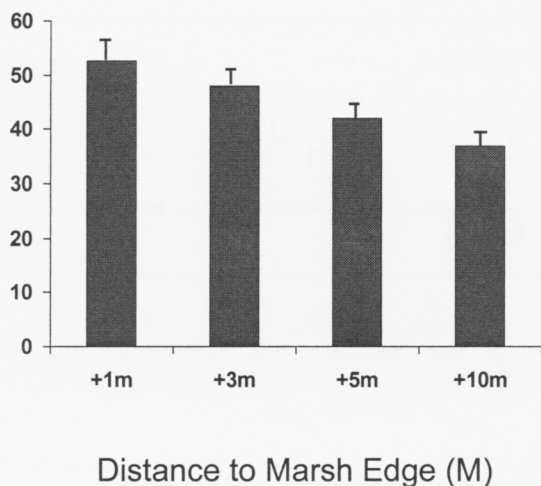


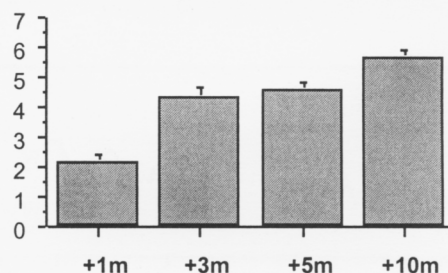
Figure 8. The least square means for the percentage of sand in each vegetated location; means represent the edge effect after removing the elevation covariate. Error bars indicate one standard error.

$p=0.001$), with highest mean values occurring at the +10m location (Figure 9). Elevation was not correlated with SOC (ANCOVA, $F_{1,96} = 0.5028$, $p=0.48$) or LMOM (ANCOVA, $F_{1,96} = 2.0048$, $p=0.16$) when both distance to the marsh edge and elevation were factors in our analysis. The amount of detritus (dead macroorganic matter) and shoot density was similar among locations and was not significantly related to elevation or distance from the marsh edge. In addition, shoot density did not vary greatly among sampling periods, and the marsh edge did not move throughout the year.

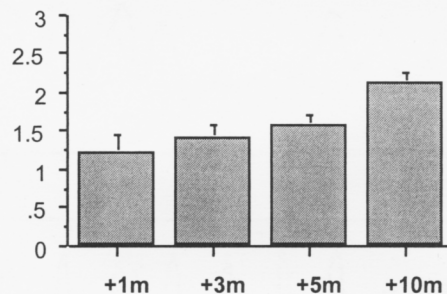
DISCUSSION

Juvenile decapod crustaceans and fishes are abundant in salt marshes of the northern Gulf of Mexico, and these nekton predators often feed on benthic infauna and epifauna from marsh sediments (Leber 1985, Hunter and Feller 1987, Minello et al. 1989, Feller 1991, Minello and Zimmerman 1991, Kneib 1997a). Coastal salt marshes in this region can be highly fragmented, with a large amount of marsh edge; densities of nekton such as juvenile penaeid shrimps, blue crabs *Callinectes sapidus* Rathbun, and some fishes are greatest in marsh vegetation within a few meters of the edge (Baltz et al. 1993, Minello et al. 1994, Peterson and Turner 1994, Minello 1999, Rozas and Zimmerman 2000, Minello and Rozas 2002). These predators move across the marsh edge from low tide refuges to forage on the vegetated marsh surface

(A) Sediment Organic Content (percentage)



(B) Living Macro-organic Matter (g)



(C) Detrital Macro-organic Matter (g)

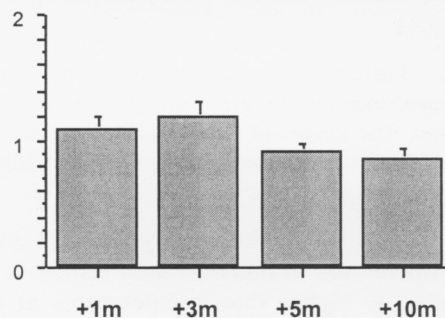


Figure 9. Amount of organic material in sediment cores collected from the four vegetated locations in July. Sediment Organic Content is the mean percentage of the weight of the core sample lost upon ignition. Macro-organic matter is the dry biomass of organic matter in sediment cores retained on the 0.5-mm sieve, and separated into living and detrital fractions. Each mean represents 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.

(Weisburg et al. 1981, Rozas and LaSalle 1990, Kneib and Wagner 1994, McTigue and Zimmerman 1998, Kneib 1997b, 2000). Juvenile brown shrimp *Farfantepenaeus aztecus* (Ives), white shrimp *Litopenaeus setiferus* (Linnaeus), and daggerblade grass shrimp *Palaeomonetes pugio* Holthuis feed extensively on surface dwelling infauna such as *Streblospio benedicti* and peracarid crustaceans such as *Hargeria rapax* (Kneib 1985, Mayer 1985, McTigue and Zimmerman 1998).

Thomas (1989) found that juvenile blue crabs also fed on peracarid crustaceans and other epiphytic organisms. *Hargeria rapax* and amphipods are common prey of transient and resident fishes in U. S. Gulf and Atlantic coast marshes (Valiela 1977, Meredith and Lotrich 1979, Kneib 1986, Minello et al. 1989, Rozas and LaSalle 1990). These infaunal species living on and near the sediment surface likely are preyed upon because they are more accessible than infauna living deeper in the sediment (Reise 1978, Stoner 1979, Virnstein 1979, Nelson and Capone 1990, Sudo and Azeta 1992, Schlacher and Wooldridge 1996). Our study provides evidence that trophic interactions with nekton predators strongly influence the distribution of surface-dwelling infauna in a salt marsh of the Galveston Bay system, Texas.

Common surface-dwelling species including *Streblospio benedicti* and *Hargeria rapax* were most abundant in low-elevation marsh edge sediments. Similar distribution patterns have been reported for these suspension and surface deposit feeders in other marsh systems (Subrahmanyam and Coultas 1980, Kneib 1984, Moy and Levin 1991), although large densities of *H. rapax* also have been reported in the high intertidal zone in Atlantic coast marshes (Reice and Stiven 1983, Kneib 1992). When we examined the relative importance of elevation and edge, distributions of these species were unrelated to elevation throughout most of the sampling year. However, there was almost always a significant negative relationship between densities of surface dwellers and distance from the marsh edge. The strength of this relationship was exemplified in May when peracarid crustacean densities were five times greater at the +1m location compared with densities in locations only two meters on either side (-1m and +3m locations).

In contrast to surface dwellers, subsurface deposit feeders (mainly oligochaetes) were more evenly distributed among our vegetated sampling locations, and mean oligochaete densities were often greatest in areas furthest from the marsh edge. Similar distributions have been observed in Atlantic coast salt marshes (Kneib 1984, Moy and Levin 1991). Throughout the year, oligochaete densities remained relatively stable, even during the dramatic decline of surface-dwellers in the late spring. Clearly, the temporal and spatial distribution patterns of oligochaetes living below the sediment surface were different than those of surface-dwelling infauna, suggesting that different factors are important in determining the distribution of these infaunal groups.

Predation pressure can be an important force in structuring estuarine infaunal prey populations (Wiltse et al. 1984, Leber 1985, Nelson and Capone 1990, Posey and Hines 1991), and this pressure may vary

seasonally and spatially in relation to predator abundance and accessibility of prey. In the winter and early spring, relatively low predator densities (Zimmerman and Minello 1984, Zimmerman et al. 1990) coincide with low water levels (Minello and Webb 1997), and nekton predation pressure on the marsh surface is relatively low. Benthic infauna and epifauna are typically most abundant during this period (Flint and Younk 1983, Zimmerman et al. 1991, Kneib 1992). We found densities of marsh infauna to be relatively high at this time despite long periods of desiccation, with the greatest densities occurring on marsh surface sediments just inside the marsh edge (+1m). The density of infauna, particularly surface-dwelling species, began decreasing in the late spring, and low densities persisted through early fall. Transient nekton predators typically recruit into the Galveston Bay system during spring (Zimmerman and Minello 1984, Zimmerman et al. 1990, Minello and Webb 1997) and obtain access to infaunal populations as increased water levels continually flood the marsh surface. These patterns suggest that seasonal changes in predation intensity were responsible for the observed decreases in infaunal populations. Caging experiments (Wiltse et al. 1984) also have provided direct evidence that predation can be responsible for seasonal decreases in marsh infaunal abundance. In addition to seasonal patterns, spatial distributions of marsh infauna support the importance of predation in the marsh. Even when the entire marsh surface is flooded, nekton densities are generally greatest near the marsh edge (Baltz et al. 1993, Peterson and Turner 1994, Minello 1999, Rozas and Zimmerman 2000). Coincident with our study on infauna, Minello and Rozas (2002) examined the fine-scale density distributions of nekton in our study marsh during spring and fall and found the greatest mean densities at 1 m from the marsh edge, just within the vegetation. Therefore, predation pressure on benthic infauna was likely greatest along the marsh edge from late spring through the fall, and the decrease in densities of surface dwelling infauna during this period was most dramatic near the marsh edge.

In addition to predation intensity, infaunal populations may be affected by environmental gradients associated with elevation and distance from the marsh-water interface. By affecting the duration and frequency of tidal flooding and desiccation, elevation affects temperature (Hummel et al. 1986), sediment drainage (Yelverton and Hackney 1986, Harvey et al. 1987), pore water salinity (Morris et al. 1990, Warren and Niering 1993), and vegetation patterns (Mendelssohn and Seneca 1980, McKee and Patrick 1988, Reed and Cahoon 1992). We found that sediment temperatures fluctuated most at the highest elevation location sampled (+10m). Thus, temperature may have limited dis-

tributions of some infauna at high elevations. Elevation has often been positively correlated with vegetation density and sediment organic levels, and these factors seem important to infaunal distribution patterns as well (Rader 1984, Lana and Guiss 1991, Sacco et al. 1994). Peterson and Black (1988), however, found that elevation, by itself, did not explain observed zonation patterns of suspension feeding bivalves on a tidal flat, and Minello et al. (1994) found that, at similar elevations, polychaete densities were related to distance from the marsh edge. Even in rocky intertidal habitats, the physiological effects of increasing elevation do not fully explain observed patterns of zonation (Peterson 1991); predation and competition along the lower portions of the elevational gradient also contribute to distribution patterns (Paine 1966, Dayton 1971, Connell 1972). Sediment grain size in our study was affected by both elevation and distance from the marsh edge, with the percentage of sand increasing towards the marsh edge. Although, sediment characteristics can affect infaunal distributions, these sediment patterns are unlikely to change seasonally and probably are not responsible for the dramatic changes in surface dwelling infauna seen in the marsh.

Our data from a Texas salt marsh suggest that both elevation of the marsh surface and distance from the marsh edge are important in influencing infaunal abundances. Predation by nekton appears to strongly influence the abundance of surface-dwelling infauna, and predation intensity changes with seasons, elevation (in conjunction with tidal flooding), and with distance from the marsh edge. Studies conducted in marshes on the Atlantic coast of the U.S. have emphasized the importance of elevation (as opposed to edge effects) in determining infaunal abundances (Kneib 1984, 1992, Moy and Levin 1991, Levin et al. 1996), but elevational differences in our marsh were relatively small (7.5 cm mean elevational change among marsh locations, $SE = 0.13$) compared with those reported for Atlantic coast marshes. Microscale tides in the Gulf and extensive inundation of the marsh surface also may reduce the effects of elevation (Rozas and Reed 1993, Minello and Webb 1997, Stumpf and Haines 1998). Brown (1995) states that "in most ecological gradients, the majority of species find one direction to be physically stressful and the opposite direction to be biologically stressful." This statement seems appropriate to describe the distributions of surface-dwelling infauna in our Galveston Bay marsh. Our results conform to a hypothetical scheme proposed by Kneib (1984) where predation by nekton control infaunal densities at low elevations near the marsh edge and the frequency and duration of tidal inundation place an upper limit on infaunal distributions within the marsh. The low elevation and frequent inundation of

sediments near the marsh edge likely promotes favorable environmental conditions for surface dwelling infauna. Tempering these beneficial conditions, however, is intense predation pressure by estuarine nekton during seasons when predators are abundant and the marsh edge is tidally inundated for extended periods. Thus, the marsh edge seems to be a dynamic interface where highly productive infaunal populations and nekton predators fluctuate dramatically with seasons. Large amounts of marsh edge are common in the degrading and highly fragmented marsh systems of the northern Gulf of Mexico, and the trophic connection between benthic infauna and nekton predators is likely important in making these systems productive for fishery resources (Zimmerman et al. 2000).

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